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Special moult of breast and belly feathers during breeding in Golden Plovers *Pluvialis apricaria*

Joop Jukema and Theunis Piersma

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Samples of breast feathers of Golden Plovers were collected from live birds captured in spring and autumn staging areas in The Netherlands. Three types of feathers were distinguished: winter and summer feathers, and a peculiar type, called the striped feather. Striped feathers were not found in spring, but made up about 20% of the feathers in samples collected in autumn. Examination of skins of birds collected on the breeding grounds showed that striped feathers develop on the breast and belly of Golden Plovers around the last week of incubation. After arrival in The Netherlands, striped as well as summer feathers are replaced by winter feathers (post-breeding moult). The moult, on the breeding grounds, of part of the ventral summer plumage to special (short-lasting) striped feathers is named the *partial breeding moult*, and appears hitherto undescribed in other birds. The appearance of striped feathers makes the summer plumage of Golden Plovers less contrasting. This leads us to propose that the balance between selection for a distinctive plumage and for camouflage changes in the course of the season and has thus lead to the evolution of this peculiar moult.

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Introduction

The sequence of body plumages of adults of the great majority of bird species follows a regular pattern of alternating non-breeding and breeding plumages, brought about by the post- and pre-breeding body moults, respectively (Ginn and Melville 1983, terminology of Cramp and Simmons 1977). Waders (Charadrii) appear to conform perfectly to this pattern (Prater et al. 1977, Hale 1980), although Ferns (1978) provided evidence that in four high arctic species, the post-breeding moult of the body plumage already commences when the birds are still incubating. This, however, only means that the labelling as post-breeding moult is descriptively not entirely accurate. In this paper we aim to document the existence of a hitherto unrecognized special (partial) moult of the ventral body plumage of Golden Plovers *Pluvialis apricaria* on the breeding grounds.

Here we do not distinguish between the two supposed subspecies of the Golden Plover (i.e. the southern ssp. *apricaria* breeding in the British Isles and around the North and Baltic Seas, and the northern ssp. *altifrons* breeding in Greenland, Iceland, the Faroes, Fennoscandia and northern Russia; Byrkjedal 1978a, Cramp 1983). This is because a complete range of intermediate forms occurs in our study area (Jukema and Boere, unpubl.; see also Parr 1980). We do, however, take differences in breeding origin into account when examining study skins, because of the large differences in the timing of breeding and moult between the two geographical populations (Byrkjedal 1978b).

Methods

Golden Plovers were captured in the west and north of the province of Friesland, The Netherlands, using a net-

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ting device especially adapted for this species, the 'wil-
snetnet' (Eenshuistra 1973, Koopman and Hulscher
1979). Immediately after capture the birds were
weighed and measured, and notes on the extent of body
moult and primary moult were taken (Jukema 1982).
Primary moult was scored with the widely used 5-point
system (Ginn and Melville 1983: Fig. 7b).

In addition, samples of 10–30 contour feathers of the
plumage on the breast were plucked from each bird
(Fig. 1). These feathers were categorized as belonging
to three main types: summer, striped, and winter feath-
ers (Fig. 1). The basic colour of summer feathers is
dark-brown to black, but the feathers may be partly
white or have a yellowish centre. The distinguishing fea-
tures of striped feathers are their yellowish vanes with
distinct brown stripes radiating from the shaft to the
feather's edge. All winter feathers are uniformly light
brown. As striped and summer feathers are both char-
acteristic of the plumage in the breeding season, they
are collectively called breeding plumage feathers. Birds,
with both breeding plumage and new winter plumage
feathers are in transitional plumage.

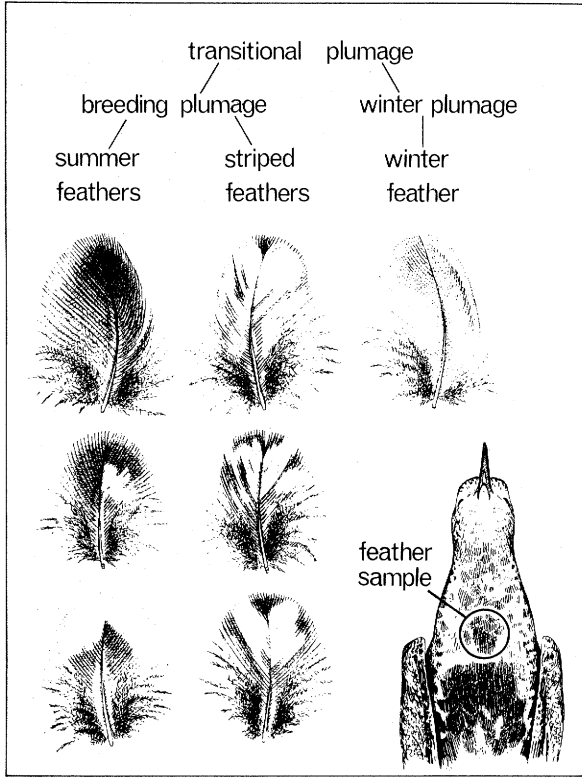


Fig. 1. Contour feather types encountered in the ventral
plumage of Golden Plovers: summer, striped and winter feath-
ers. The three sub-types of summer feather are shown on the
left, whereas the variation in striped feathers is shown in the
middle. The plumage terminology used in this paper is shown
in the top. The location on the bird where breast feather sam-
ples were collected is also depicted.

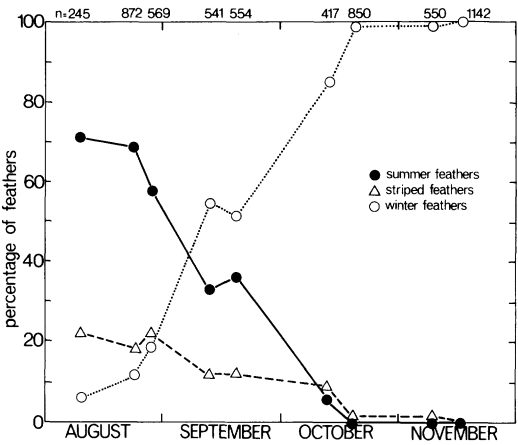


Fig. 2. Relative occurrence of different contour feather types in
breast feather samples of Golden Plovers captured in The Nether-
lands in autumn 1985. n (above diagram) refers to the
number of feathers examined.

In order to interpret the observations on live birds
captured during migration and wintering in the Nether-
lands, a series of skins of birds collected on the British
and Scandinavian breeding grounds was also examined.

Results

Examination of migrants

None of the 533 feather samples of Golden Plovers col-
lected in spring contained striped feathers. However,
upon their return from the breeding grounds, from the
second half of July onwards, an increasing percentage of
Golden Plovers had striped feathers among their breast
feathers. Of about 850 individual striped feathers exam-
ined, only two were 'in sheath' (i.e. being moulted),
which strongly suggests that Golden Plovers do not de-
velop this type of contour feather during autumn mi-
gration but while on the breeding grounds. In August
over 20% of the breast feathers belonged to the 'striped'
category (Fig. 2), but both the percentage striped, and
the percentage summer feathers declined in the course
of the autumn, giving way to winter feathers.

The occurrence in autumn of striped feathers in indi-
vidual birds is examined in more detail in Fig. 3. Al-
though the percentage of birds in full breeding plumage
drops to little more than zero in early September, the
percentage of birds with one or more striped feathers
remains at more than 50% until mid October (Fig. 3A).
From the end of October onwards, 90% or more of the
birds are in full winter plumage; the few birds in tran-
sitional plumage still have one or more striped feathers
but no summer feathers. Fig. 3B shows that in the
course of the season an increasing percentage of the
birds in transitional plumage had striped feathers next
to winter feathers. This indicates that striped feathers,
in comparison with summer feathers, are replaced by

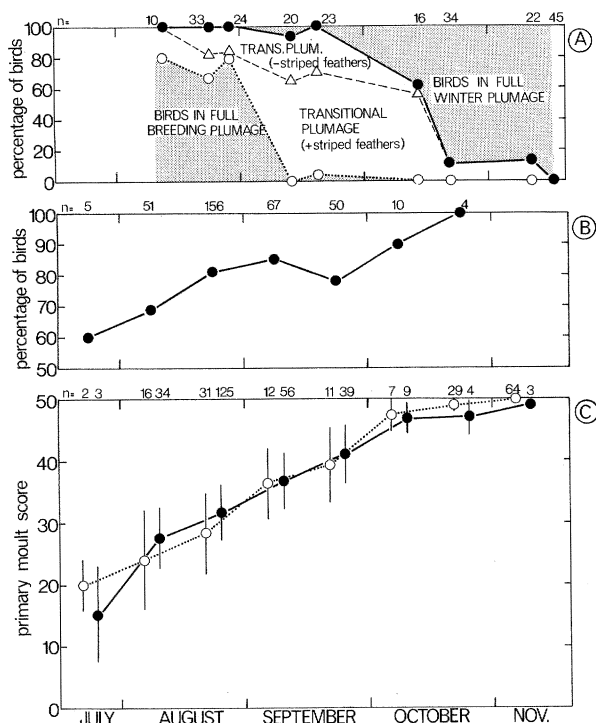


Fig. 3. Occurrence of striped feathers in breast samples of Golden Plovers in The Netherlands in relation to the time of the year (A, B) and primary moult (C). (A) shows the relative occurrence in the course of the autumn of birds with one or more summer and/or striped feathers (solid dots), with one or more striped feathers (triangles), or with only summer- and/or striped feathers (open dots). (B) shows the percentages of birds with breeding plumage feathers, including at least one striped feather. (C) shows the average primary moult scores (± 1 S.D. for birds with (solid dots) and without (open dots) striped feathers, in the course of the season. The data in (A) were collected in 1985 only, and are presented per capture-date, whereas the data in (B) and (C) were collected in 1982, 1983 and 1985 and are presented per half month period. n (above each diagram) refers to the number of individuals examined.

winter feathers relatively late in the season. Until half-way through October there were no differences in the progress of primary moult between birds with, and birds without striped feathers (Student's t-tests, $p > 0.05$). In the second half of October and in early November though, the birds which had not completed their primary moult, were always the ones which still had one or more striped feathers in their breast feather samples.

The theoretical possibility that the autumn occurrence of striped breast feathers in Golden Plovers captured in The Netherlands is due to the presence of different breeding populations in spring and in autumn, can be dismissed by the observations on individual birds captured in both spring and autumn; in all three cases, striped feathers were present in breast feather samples from the autumn and not in those from spring (Fig. 4).

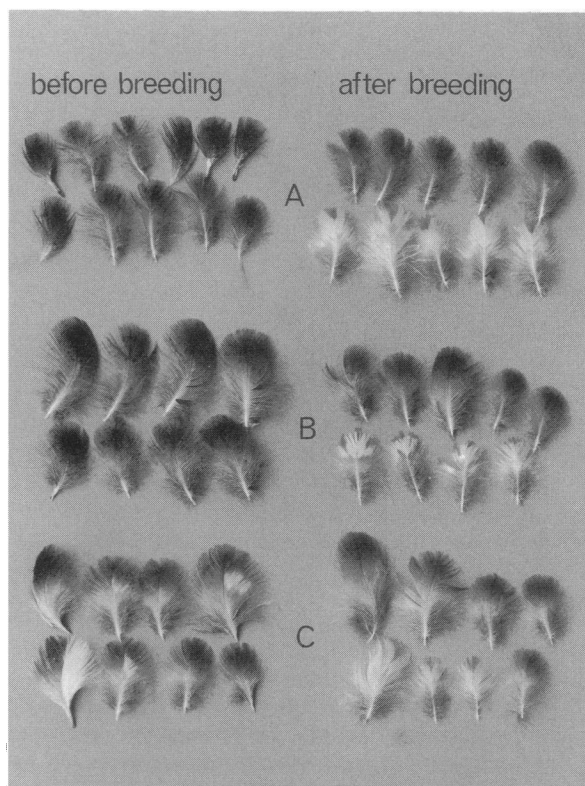


Fig. 4. Photographic evidence that striped feathers are only present in the ventral body plumage of Golden Plovers after the return from the breeding grounds (for each bird, striped feathers are shown in the lower row, to the right). Plover A was captured on 14 April 1984 and 24 August 1982; plover B on 18 April 1983 and 9 September 1984 and plover C on 14 April 1985 and 31 August 1983. Winter feathers are not shown.

Examination of birds from the breeding grounds

The observations on the occurrence of striped feathers in birds captured in the Netherlands are nicely amplified by the results of examination of study skins from the breeding areas (Tab. 1). Both birds collected on typical *apricaria* (southern) and typical *altifrons* (northern) breeding areas showed striped feathers. In the sample of birds from the southern breeding areas, however, only males (darkest!) showed striped feathers. Tab. 1 also shows that only northern birds belong to the category 'many' striped feathers. Since all southern birds retain some old winter feathers in their breeding plumage, which already give them a rather speckled appearance, growing striped feathers may not change their plumage much.

According to Byrkjedal (1978b) and Parr (1980), eggs of Golden Plovers from southern breeding areas hatch between mid May and mid June. As the first striped feathers appear in a southern bird collected on 13 May, in a second bird on 27 May, this indicates that southern Golden Plovers develop striped feathers just

Tab. 1. Occurrence of striped feathers and newly grown winter feathers in museum skins of birds collected in breeding areas occupied by the southern and the northern 'subspecies' of Golden Plover (*P. a. apricaria* and *P. a. alifrons*; see text). The stage of primary moult is indicated by the number of old (unshed) primaries. Few = 0–10, many >10 feathers. F = female, M = male.

Date of collection	Sex	No. of old primaries	Striped feathers			New winter	
			no	few	many	no	few
<i>Southern breeding area</i>							
15 Apr	F	10	×			×	
7 May	M	10	×			×	
13 May	M	10		×		×	
13 May	M	10	×			×	
16 May	F	10	×			×	
16 May	F	10	×			×	
24 May	M	10	×			×	
24 May	F	10	×			×	
26 May	M	10	×			×	
27 May	M	10	×			×	
27 May	M	8		×		×	
3 Jun	F	10	×			×	
3 Jun	F	10	×			×	
4 Jun	M	10		×		×	
4 Jun	M	10	×			×	
18 Jun	M	7		×		×	
19 Jun	M	7		×		×	
20 Jun	M	7		×		×	
<i>Northern breeding area</i>							
? Jun	M	10	×			×	
10 Jun	M	10	×			×	
13 Jun	M	10	×			×	
25 Jun	F	8	×			×	
26 Jun	M	9		×		×	
28 Jun	M	7		×		×	
7 Jul	F	9		×		×	
9 Jul	M	8	×			×	
10 Jul	M	7		×		×	
12 Jul	F	10	×			×	
13 Jul	F	6		×			×
21 Jul	F	5		×		×	
22 Jul	M	7		×		×	
22 Jul	M	6		×		×	
22 Jul	F	5		×		×	
22 Jul	M	5			×	×	
22 Jul	M	5			×	×	
22 Jul	F	4		×			×
22 Jul	M	4			×	×	
28 Jul	M	3		×		×	
7 Aug	M	4		×		×	
8 Aug	M	3		×			×
9 Aug	M	4		×		×	
9 Aug	M	3		×		×	
16 Aug	M	4		×			×
16 Aug	M	4		×			×
16 Aug	M	3		×		×	
16 Aug	M	3		×			×
16 Aug	M	3		×			×
23 Aug	M	4		×			×
23 Aug	M	3		×			×
24 Aug	F	4		×			×
30 Aug	M	4		×			×

before or around the time their eggs hatch. This is further supported by birds from northern breeding areas, which first show striped feathers in late June/early July, i.e. just before their eggs hatch (2nd and 3rd week of July; Byrkjedal 1978b).

According to Byrkjedal (1978b) the primary moult in Norway starts in early July, both in the northern and in the southern breeding populations. This is during incubation in the northern, and after hatching in the southern populations. (C. Thomas (in litt.) has pointed out that in Great Britain many (southern) Golden Plovers start primary moult in mid June, during incubation.) The local differences in the timing of primary moult in Norway are reflected in the relationship between the appearance of striped feathers and the onset of primary moult (Tab. 1). Whereas in birds from northern breeding areas the appearance of striped feathers and the onset of primary moult seem to coincide, this is clearly not always the case in birds from the southern population, from which two out of six birds show striped feathers without having started primary moult. We therefore suggest that there is no direct physiological connection between the onset of primary moult and the development of striped feathers.

Close examinations of study skins and of live birds in the hand, revealed that when striped feathers occur on a bird, their densities are highest on the flanks near the white band around the black breast and belly patch. We have not quantified this phenomenon, however.

Discussion

We have shown that a distinctive type of contour feather develops in the breeding plumage of Golden Plovers at about the last week of incubation. This feather type replaces up to a quarter of the initial breeding plumage feathers on the breast. Here we ask whether this type of *partial breeding moult* has been described for other bird species before. Sauer (1962) and Johnson and Johnson (1983) found that Lesser Golden Plovers *P. dominica* started body moult during incubation. Sauer (1962) incorrectly labeled the moult between breeding and winter plumage as a moult into 'eclipse' plumage. (The 'eclipse' plumage of Anatidae is nothing but a non-breeding (i.e. winter) plumage worn for a relatively short time in summer, which is replaced in autumn by an (early) breeding plumage; see Oring 1968, Young and Boag 1981.) Ferns (1978) also found that four other waders breeding in the high arctic (Ringed Plover *Charadrius hiaticula*, Sanderling *Calidris alba*, Dunlin *C. alpina* and Turnstone *Arenaria interpres*) showed body moult during incubation and while tending their young. The above authors all interpreted this moult as a post-breeding moult (a moult from summer to winter plumage). This may have been true, but it should be noted that the development of a special feather type like the striped feather of Golden Plovers is easily overlooked. Therefore, although we are not aware of any

other well established example, we suggest that a comparable partial breeding moult may well be found in (wader) species other than the Golden Plover, if looked for.

The existence of such a special moult of body feathers, a moult which does not fit in with the 'normal' moult schedules of temperate bird species (Ginn and Melville 1983), implies that there must be strong selective pressures leading to its evolution. In an attempt to define the probable functional context, the following points were taken into account:

- in a Scottish study area, male Golden Plovers with the darkest plumage occupied the best breeding habitat, were most often the winners in aggressive encounters between males, and were paired with the darkest females (Edwards 1982). A contrasting plumage pattern is therefore important for territory establishment;
- the onset of the partial breeding moult probably occurs in the last week before hatching and will thus have proceeded considerably by the time when the adults take care of the young (especially the males, on the northern breeding areas; Byrkjedal 1978b);
- during incubation, the reaction to ground predators is either to steal away from the nest at more than 100 m distance from the predator and remain silent and out of view, or to sit tight (if the predator is discovered at shorter distance) and flush from the nest at a distance of 8-10 m and perform distraction display (Byrkjedal pers. comm.);
- in late incubation or when tending young, Golden Plovers disturbed by predators tend to leave the immediate surroundings of the nest or young by an inconspicuous 'rodent-run', before starting calling, mobbing, or injury-feigning (Byrkjedal 1978a, Cramp 1983);
- light and more uniformly coloured 'southern' birds tend to occur in more uniform breeding habitats (e.g. moorland) than 'northern' birds with a darker and more contrasting ventral plumage. The latter breed in 'discontinuous' habitats such as stony tundra, which are often rather contrast-rich due to the patchy occurrence of whitish lichens and stones (Ratcliffe 1976, Byrkjedal 1978, pers.comm.);
- in the course of the season, the northern habitats may also become more uniform due to the disappearance of snow (Byrkjedal 1980), the growth of the vegetation (hiding stones and lichen patches) and a tendency for the weather to be less sunny and the light to become more diffuse (J. Fjelds , pers. comm.);
- males (the sex with the most contrasting plumage) tend to incubate during the day (when light intensity is highest and contrasts are most pronounced), whereas females, which are duller, incubate during the night (Parr 1980, Byrkjedal 1985);
- birds with the darkest plumage tend to show the heaviest partial breeding moult (above; see also Sauer 1962);

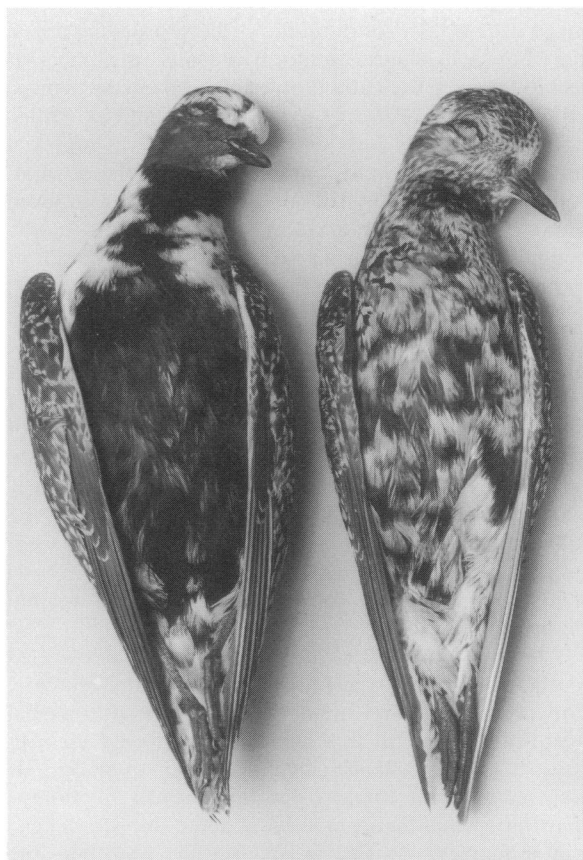


Fig. 5. Illustration of how the presence of striped breast and belly feathers alters the contrast of the ventral body plumage of male Golden Plovers. The left bird (Zool. Mus. Amsterdam 36194) was accidentally killed during capture on 28 April 1985 and the right bird (ZMA 36193, with striped feathers) on 27 August 1985.

- the appearance of striped feathers (with highest densities near the edge of the black and white transition of the breast and belly patch) leads to the development of a much less contrasting ventral plumage than before. This phenomenon is illustrated in Fig. 5.

The above series of arguments leads us to the following view of the functional context of the partial breeding moult of (northern) Golden Plovers: In early spring unpaired Golden Plovers return to their tundra-like breeding habitats where large expanses of snow alternate with dark patches of open ground. A dark and distinctive plumage is of great importance during pair formation, as it apparently signals high status. In northern habitats, the contrasts due to lichens and stones in the snow-free patches of ground where the plovers settle to breed, may 'allow' them to have a fairly distinct plumage during breeding (more so than in southern, more uniform, habitats). In the course of the season the value of a distinctive plumage for intraspecific communicative pur-

poses might decrease and therefore a more cryptic plumage develop. In addition, in northern breeding areas, the change to a more uniform plumage might be selected for since the habitat probably also becomes more uniform in the course of the summer. The risk of discovery by visually hunting predators such as raptorial birds, corvids and gulls, enforces the importance of always being cryptically coloured. For this reason, those Golden Plovers that develop striped feathers in the course of the season become or remain most difficult for predators to spot and have highest reproductive success.

We henceforth view the partial breeding moult as the outcome of a shift, in the course of the season, in the balance between advantages gained from a distinct breeding plumage and the need for camouflage, in a habitat which shows a seasonal decrease in the level of contrast. In the words of Ferns (1978): 'In Greenland, the moult of the neck was particularly heavy in the early stages in both *Ch. hiaticula* and *A. interpres*, whilst the moult of breast started early in *C. alba*. It may be significant that moult of these particular areas of the body tends to reduce the conspicuousness of the nuptial plumage'.

Obviously, our line of argument only holds if striped feathers are more cryptic than 'normal' winter feathers. For this we have no evidence, but if not true, a partial post-breeding moult to winter feathers would seem to suffice, and, mechanistically, be easier to realize. I. Byrkjedal (pers. comm.) put forward the hypothesis that this special moult may be to avoid abrasion of the winter feathers. During incubation and brooding, the abrasion of ventral feathers may be particularly great, due to frequent contact with the substrate (mountain vegetation is mostly quite stiff and hard). An abraded winter plumage could be disadvantageous to the Golden Plovers on their cold and windy European wintering grounds (Kersten and Piersma 1987). In this context it is noteworthy that, especially along the edges of the vanes, the striped feathers are more pigmented than the winter feathers, making them more resistant to abrasion. An interspecific comparison of the moult patterns of waders from high arctic breeding areas but wintering in temperate vs subtropical areas, may provide a test of the 'abrasion hypothesis'.

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